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SIMON HENRY GAGE,

VICE-PRESIDENT SECTION F,

BEFORE THE

SECTION OF BIOLOGY,

AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE.

At the Rochester Meeting,

August, 1892.

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THE COMPARATIVE PHYSIOLOGY OF RESPIRATION.

AMONG the very first of the physiological acts observed were those of respiration. The regular movements of breathing, from the first feeble efforts of the new-born babe until the sigh in the the last breath of the dying—after which is silence, cold, and dissolution—have commanded the attention and claimed the interest of every one, the thoughtful and the thoughtless alike. And one comes to feel that in some mysterious way "the breath is the life." But in what way does breathing subserve life or render it possible? Aristotle and the naturalists of the olden time supposed that it was to cool the blood that the air was taken into the lungs, and, as they supposed, also into the arteries. With the limited knowledge of anatomy in those early days, and the fact that after death the arteries are wholly or almost wholly devoid of blood, while the veins are filled with it, what could be more natural than to suppose that the arteries were vessels for the cooling air? If one supposes that he has entirely outgrown this view of Aristotle, let him think for a moment how he would express the fact that an individual is descended from the Puritans, for example. In expressing it even the physiologist could hardly bring himself to say other than "he has the blood of the Puritans in his *veins*." Would he ever say "he has the blood of the Puritans in his *arteries?*"

As observation increased, the cold-blooded animals were more carefully studied and found to possess also a respiration; they certainly do not need it to cool the blood. Then there are the insects and the other myriads of living forms that teem in the oceans,

lakes, rivers and even in the wayside pools. Do these, too, have a breath? And the plants on the land and in the water, is the air vital to them? Aristotle and the older naturalists could not answer these questions. To them, on the respiratory side at least, all life was not in any sense the same.

It was not till chemistry and physics were considerably developed, not until the air-pump, the balance and the burette were perfected that it was possible to give more than a tentative answer. Not until the microscope could increase the range of the eye into the fields of the infinitely little, was it possible to form even an approximately correct conception. The first glimmering of the real significance of respiration for all living things was in the observation that the air which would not support a flame, although it might be breathed, could not support life. That is, there must be something in the transparent air that feeds the flame and becomes the breath of life, the real *pabulum vitæ*, the merely mechanical action of the air not being sufficient.

Since the experiments on insects and other animals with the air-pump, by Boyle (1670) by Bernuilli on subjecting fishes to water out of which all the air had been boiled, and those of Mayow (1674), it became more and more evident that respiration was not confined to the higher forms, but was a universal fact in the organic world. Then came the most fruitful discoveries of all, made by the immortal Priestley (1775–6), viz., that the air is not an element but composed of two constituents: Nitrogen, which is inert in respiration, and Oxygen, which is the real vital substance of the air, the substance which supports the flame of the burning candle and the life of the animal as well.

What would seem more simple at this stage of knowledge than that the parallel between the burning candle and the living organism should be thought to represent truly the real conditions? that as the burning candle consumes the oxygen and gives out carbon dioxide, so the living thing breathes in oxygen and in place of that consumed gives out carbon dioxide. And as in each case heat is produced, what would be more natural than to look upon respiration as a simple combustion? This was the generalization of Lavoisier (1780–1789). As he saw it, the oxygen entered the lungs, reached the blood and burned the carbonaceous waste there found and was immediately given out in connection with the carbon with which it had united; and as the gas given off in a burning

candle makes clear lime water turbid, so the breath produces a like turbidity.

But here, as in many of the processes of nature, the end products or acts were alone apparent, and while the fundamental idea is probably true that respiration is, in its essential process, a kind of combustion or oxidation, yet the seat of this action is not the lungs or blood. If the myriads of microscopic forms are considered, these have no lungs, no blood, and many of them even no organs,—they are, as has been well said, — organless organisms; and yet every investigation since the time of Vinci and Von Helmont, Boyle and Mayow have rendered it more and more certain that every living thing must be supplied with the vital air or oxygen and that this is in some way deteriorated by use; and the nearer investigation approaches to the real life stuff or protoplasm, it alone is found to be the true breather, the true respirer. And further, as was shown long ago by Spallanzani (1803–1807), if one of the higher animals, as a frog, is decapitated and some of its muscle or other tissue exposed in a moist place, it will continue to take up oxygen and give out carbon dioxide, thus apparently showing that the tissues of the highly organized frog, may, under favorable conditions, absorb oxygen directly from the surrounding medium, and return to it directly, the waste carbon dioxide. This proves conclusively that it is the living substance which breathes, and that the elaborate machinery of lungs, heart and blood-vessels is only to make sure that the living matter, far removed from the external air, shall not be suffocated. Still more strange, it has been found that, if some of the living tissue is placed in an atmosphere of hydrogen or nitrogen entirely devoid of oxygen, it will perform its vital functions for a while, and although no oxygen can be obtained, it will give off carbon dioxide as in the ordinary air. If it is asked, "how can these things be?" the answer is apparently plain and direct. Not as the oxygen unites directly with the carbon n the burning candle, does it act in the living substance. The oxidations are not direct in living matter, as in the candle; but the living matter first takes the oxygen and makes it an integral part of itself, as it does the carbon and nitrogen and other elements; and finally when energy is to be liberated, the oxidation occurs, and the carbon dioxide appears as a waste product.

The oxygen that is breathed to-day, like the carbon or the nitrogen that is eaten, may be stored away and represent only so much

potential energy to be used at some future time in mental or physical action.

So far only living animal substance has been discussed. If plants are considered, what can be said of their relations to the air? The answer was given in part by Priestley (1771) who found that air which had been vitiated by animal respiration became pure and respirable again by the action of green plants. He thus discovered the harmonizing and mutual action of animals and plants upon the atmosphere; and there is no more beautiful harmony in nature. Animals use the oxygen of the air and give to it carbon dioxide which soon renders it unfit for respiration; but the green plants take the carbon dioxide, retain the carbon as food and return the oxygen to the air as a waste product. This is as thoroughly established as any fact in plant physiology; and vet in his work Priestley had some which he called "bad experiments;" for instead of the plants giving out oxygen and purifying the air, they sometimes gave off carbon dioxide, and rendered it more impure after the manner of an animal. What investigator cannot sympathize with Priestley when he calls these "bad experiments?" They appeared so rudely to put discord into his discovered harmony of nature. But nature is infinitely greater than man dreams. The "bad experiments" were among the most fruitful in the history of scientific discovery. Ingenhausz (1787) followed them up, carefully observing all the conditions, and found that it was only in daylight that green plants gave out oxygen; in darkness or insufficient light they conducted themselves like animals, taking up oxygen and giving out carbon dioxide. Finally it was proved by Saussure (1804) and others that both for green plants, and those without green like the mushrooms oxygen is as necessary for life as for animals. It thus became evident that this use of oxygen and excretion of carbon dioxide was a property of living matter, and that the very energy which in the green plant set free the oxygen of the carbon dioxide was derived from oxidations comparable with those giving rise to energy in animals. Further that the purification of the air by green plants in light is a separate function—a *chlorophyll function*, as it has been happily termed by Bernard—and resembles somewhat digestion in animals, the oxygen being discarded as a waste product. Indeed so powerful is the effort made to obtain oxygen for the life processes by some of the lowest plants—the so-called organized ferments,—that some of the most

useful and some of the most deleterious products are due to their respiratory activity. In alcoholic fermentation, as cleary pointed out by Pasteur and Bernard, the living ferment is removed from all sources of free oxygen and in the efforts of the ferment for respiration the molecules of the sugar are decomposed or rearranged and a certain amount of oxygen set free; and this oxygen supplies the respiratory needs of the ferment.

It has been found that the motile power of some bacteria like *Bacterium termo, e. g.*, depends on the presence of free oxygen in the liquid containing them. When this is absent they become quiescent. This fact has been utilized by Engelmann and others in the study of the evolution of oxygen by green and other colored water plants. The bacteria serve as the most delicate imaginable oxygen test, so that when the minutest green plant is illuminated by sufficient daylight, the previously quiescent bacteria move with great vigor and surround it in swarms. Out of the range of the plant the bacteria are still or move very slowly as if to conserve the minute energy-developing substance they have in store until it can be used to the best advantage.

May we not now approach the problem directly and answer, for the whole organic, living world, the question, "what is respiration?" by saying *it is the taking up of oxygen and giving out of carbon dioxide by living matter.* This is the universal and essential fact with all living things whether they are animals or plants, whether they live in the water or on land. But the ways by which this fundamental life process is made possible, the mechanisms employed to bring the oxygen in contact with the living matter and to remove the carbon dioxide from it are almost as varied as the groups of animals; each group seems to have worked out the problem in accordance with its special needs. It is possible, however, in tracing out these complex and varied methods and mechanisms, to recognize two principal ones,—*The Direct and the Indirect.*

In the first, there is the direct assumption of oxygen from the surrounding medium, and the excretion of carbon dioxide directly into it. The best examples of this are presented by unicellular forms like the amœba where the living substance is small in amount and everywhere laved by the respiratory medium. But as higher and higher forms were destined to appear, evidently the minute, organless amœba could not in itself realize the great aim toward which Nature was moving. There must be an aggregation of

amœbas, some of them serving for one purpose and some for another. Like human society, as civilization advances, each individual does fewer things, becomes in some ways less independent, but in a narrow sphere acquires a marvelous proficiency. Or, to use the technical language of science: *In order to advance there must be aggregation of mass, differentiation of structure and specialization of function.* Evidently, however, if there is an aggregation of mass, some of the mass is liable to be so far removed from the supply of oxygen and the space into which carbon dioxide can be eliminated that it is liable to be starved for the one and poisoned by the other. Nature adopted two simple ways to obviate this: First, to form its aggregated masses into a kind of network or sponge with intervening channels through which a constant stream of fresh water may be made to circulate, so that each individual cell of the mass could take its oxygen and eliminate its carbon dioxide with the same directness as its simple prototype, the amœba.

But in the course of evolution forms appeared with aërial respiration; and the insects, among these, solved the mechanical difficulty of respiration by a most marvelous system of air tubes or tracheæ extending from the free surface, and therefore from the surrounding air, to every organ and tissue. By means of this intricate network air is carried and supplied almost directly to every particle of living matter. The respiration is not quite direct with the insects, however, for the oxygen and carbon dioxide must pass through the membranous wall of the air tube before reaching or leaving the living substance.

In the next and final step, the step taken by the highest forms, the living material is massed, giving rise not only to animals of moderate size, but to the huge creatures that swim in the seas like the whale or walk the earth like the elephant. With all of these the step in the differentiation of the respiratory mechanism consists in the great perfection of lungs or gills, and in the addition of a complicated circulatory system with a respiratory blood, one of the main purposes being, as the name indicates, to subserve in respiration by carrying to each individual cell in the most remote and hidden part of the body the vital air, and in the same journey removing the poisonous carbon dioxide.

This has been called *Indirect Respiration*, because the living matter of the body does not take its oxygen directly either from air or water, but is supplied by a middle man, so to speak.

The complicated movements by which water is forced over the gills, or by which the lungs are filled and emptied, and the great currents of blood are maintained, that is, the striking and easily observed phenomena of respiration are thus seen to be only superficial and accessory; they only serve as agents by which the real and the essential processes that go on in silence and obscurity are made possible.

So far I have attempted to give a brief résumé of the views on respiration that have been slowly and laboriously evolved by many generations of physiologists, each adding some new fact or correcting some misconception; and I trust that this brief sketch has recalled to your minds the salient facts in our knowledge of respiration, and that it will give a just perspective, and enable me, if I may be permitted, to describe briefly what I believe to be my own contribution to the ever-accumulating knowledge of this subject.

In 1876–1877, Professor Wilder, who may be said to have inherited his interest in the ganoid fishes directly from his friend and teacher, Agassiz, who first recognized and named the group, was studying the respiration of the forms *Amia* and *Lepidosteus*, common in the great lakes and the western rivers. As his assistant it was my privilege to aid in the experiments, and thus to acquire the spirit and methods of research in the most favorable way, by following an investigation by a master from its beginning to its close. The results of that inquiry were reported to this section in 1877, and formed a part of the Proceedings of the Association for that year. From that time till the present the problems of respiration in the living world have had an ever increasing fascination for me and no opportunity has been lost to investigate the subject. The interest was greatly increased by the discovery that a reptile—the soft-shelled turtle—did not conform to the generalizations in all the treatises and compendiums of zoölogy, which state with the greatest definiteness that all reptiles, without exception, are purely air breathing, and throughout their whole life obtain oxygen from the air and never from the water. The American soft-shelled turtles, *Amyda* and *Aspidonectes*, at least, do not conform to this generalization, but on the contrary naturally and regularly breathe in the water like a fish as well as in the air like an ordinary reptile, bird, or mammal.

In carrying on the investigation of the respiration of the turtle there appeared for solution the general problem, which briefly stated

is as follows:—In case an animal breathes both in the air and in the water, or more accurately, has both an aërial and an aquatic respiration like the Ganoid fishes *Amia* and *Lepidosteus*, like the soft-shelled turtles, the tadpoles and many other forms, what part of the respiratory process is subserved by the aqueous and what by the aërial portion of the apparatus? So far as I am aware this problem had not been previously considered. It was apparently assumed that there were in these fortunate animals two independent mechanisms, both doing precisely the same kind of work, that is, each serving to supply the blood with oxygen and to relieve it of carbon dioxide as though the other were absent. That was a natural inference, for with many forms the respiration is wholly aquatic, all the oxygen employed being taken from the water and all the carbon dioxide excreted into it. On the other hand in the exclusively air breathing animals, as birds and mammals, the respiration is exclusively aërial.

This natural supposition was followed in the first investigations on the respiration of the soft-shelled turtles, and while it was proved with incontestable certainty that they take oxygen from the water like an ordinary fish, that is, have a true aquatic respiration in addition to their aërial respiration, there was altogether too much carbon dioxide in the water to be accounted for by the oxygen taken from it. Furthermore, upon analyzing the air from the lungs of a turtle that had been submerged sometime, the oxygen had nearly all disappeared and but very little carbon dioxide was found in its place, whereas by analogy with human respiration for example, a quantity of carbon dioxide nearly as great as that of the oxygen which had disappeared should have been returned to the lungs. Likewise in Professor Wilder's experiments with *Amia*, to use his own words: "Rather more than one per cent. of carbon dioxide is found in the normal breath of the *Amia;* but much more of the oxygen has disappeared than can be accounted for by the amount of carbon dioxide." Everything thus appeared anomalous in this mixed respiration, and instead of a clear, consistent and intelligible understanding of it there seemed only confusion and ambiguity. Truly these seemed like "bad experiments."

It became perfectly evident that the first step necessary in clearing the obscurity was to separate completely the two respiratory processes, to see exactly the contribution of each mechanism to the total respiration. But this was no easy thing to do. In the first

place the animal must be confined in a somewhat narrow space in order that air and water which are known to have been affected by its respiration may be tested to show the changes produced in it by the respiratory process; in the second place the water has so great a dissolving power upon carbon dioxide that even if it were breathed out into the air it would be liable to be absorbed by the water; then some means must be devised to prevent the escape of the gases from the water as their tension becomes changed; and, finally, as the animal in the water must be able to reach the air, a diaphragm must be devised which would prevent the passage of gases between the air and the water, and at the same time offer no hindrance to the animal in projecting its head above the water. As a liquid diaphragm must be used it occurred to me that some oil would serve the purpose; but the oil must be of a peculiar nature, it must not allow any gases to pass from air to water or the reverse, it must not be in the least harmful or irritating to the animal under experimentation and, finally, it must itself add nothing to either air or water. Olive oil was thought of and later the liquid paraffins. The latter were found practically impervious to oxygen and fulfilled all the other requirements, but unfortunately they absorb a considerable quantity of carbon dioxide. Pure olive oil was finally settled upon as furnishing the nearest approximation to the perfect diaphragm sought.[1]

The composition of the air being known, and a careful determination of the dissolved gases in the water having being made, the animal was introduced into the jar and the water covered with a layer of olive oil from ten to fifteen millimeters thick. The top of the jar was then vaselined, and a piece of plate glass pressed down upon it thus sealing it hermetically. Two tubes penetrate this plate-glass cover, one connecting with the overlying air chamber and the other extending into the water nearly to the bottom of the jar. As the water and air were limited in quantity the shorter the time in which the animal remained in the jar the more nearly normal would be the respiratory changes; the experiments were therefore continued only so long—one or two hours—as was found necessary to produce sufficient change in the air and the dissolved gases of the water to render the analyses unmistakable.

Proceeding with the method just described, the results given in the following table were obtained:

[1]See Wm. Thörner on the use of olive oil for the prevention of the absorption of carbon dioxide. Repertorium der analytischen Chemie, 1885, pp. 15–17.

Table of mixed Respiration, showing the number of cubic centimeters of oxygen removed from air and water, and the amount of carbon dioxide added to the air and the water per hour and kilogram.

	OXYGEN		CARBON DIOXIDE	
	FROM AIR	FROM WATER	TO AIR	TO WATER
Ganoid Fish (*Amia calva*)	65	10	22	53
Tadpoles (*Larval Batrachia*)	70	5	24	51
Soft-shelled Turtle (*Amyda mutica*)	31	8	10	29
Bull Frog (*Rana catesbiana*)	183	4	110	77

The oxygen from both the water and the air and the carbon dioxide in the air, were determined with exactness in all the experiments; but owing to the failure of some steps in the titration for the carbon dioxide in the water, the figures given for the Amia and the soft-shelled turtle are the calculated results, assuming that the respiratory quotient is one, as that is the relation found by analysis in the other case-. This table will be greatly extended when the results of the investigation now in progress are published.

It requires but a glance at the figures in this table to see that the aërial differs markedly from the aquatic part of the respiration. Even in the frog, in which the skin forms the only aquatic respiratory organ, the tendency is marked. The law appears to be unmistakably this, viz., *that in combined aquatic and aërial respiration, the aërial part is mainly for the supply of oxygen and the aquatic part largely for the excretion of carbon dioxide.* This law which I stated in 1886 has been confirmed by the repetition of old experiments and by many new ones made during the present summer. It is also confirmed by the experiments made on Lepidosteus in a different way by Dr. E. L. Mark, and published in 1890. I therefore feel confident that this is the expression of a general physiological law in nature.

From the standpoint of evolution we must suppose that all forms originated from aquatic ancestors, whose only source of oxygen was that dissolved in the water. As the water is everywhere covered with the limitless supply of oxygen in the air—there being 209 parts of oxygen in 1000 parts of air as contrasted with the 6 parts of oxygen dissolved in 1000 parts of water—it is not difficult to conceive that in the infinite years the animals found by necessity and experience that the needed oxygen was more abundant in the overlying air, and that some at least would try more and more to make use of it. And as any thin membrane with a plentiful blood supply may serve as a respiratory organ to furnish

the blood with oxygen, it is not impossible to suppose that such a membrane, as in the throat, could modify itself little by little with ever increasing efficiency; and that one part might become especially folded to form a gill and another might become saccular or lung-like to contain air. While I am no believer in the purely mechanical physiology which sees no need of more than physics and chemistry to render possible and explain all the phenomena of life, yet it is patent to every one that, although vital energy is something above and beyond the energies of physics and chemistry, still it makes use of these; and certainly dead matter forms the material from which living is built. So, given a living thing, it, in most cases, moves along lines of least, rather than of greatest resistance; therefore, if a practically limitless supply of oxygen may be obtained from the air and only a limited amount from the water, if any thing that might serve as a lung is present, most naturally the animal will take the oxygen from the air where it is in greater abundance and more easily obtained. On the other hand, carbon dioxide is so soluble in water that practically an unlimited amount may be excreted into it; and as it is apparently somewhat easier, other things being equal, for it to pass from the liquid blood to the water than to the air, it seems likewise natural that the gills should serve largely for the excretion of the carbon dioxide into the water. This is the actual condition before us in these, and I believe in all other cases, of mixed or of combined aërial and aquatic respiration. And I believe, as stated above, the law in respiration is, that where-ever both water and air are used with corresponding respiratory organs *the aërial part of the respiration is mainly for the supply of oxygen, and the aquatic part largely for the getting rid of carbon dioxide.*

It is not difficult to see in an actual case like that of the Ganoid Fishes (*Amia* and *Lepidosteus*) the logical steps in its evolution, by which this most favorable condition has been reached; a condition rendering these fishes capable of living in waters of almost all degrees of purity, and thus giving them a great advantage in the struggle for existence. But what can be said of the soft-shelled turtles, animals belonging to a group (Reptilia) in which purely aërial respiration is almost exclusively the rule? Standing alone, this might be exceedingly difficult or impossible of explanation. The Batrachia (frogs, toads, salamanders, etc.), all have gills in their early or larval stage, and most of them develop in the

9. Mark, E. L. Studies on Lepidosteus. Part I. Bulletin of the Museum of Comparative Zoölogy, Harvard University, Vol. xix (1890). Respiration is discussed on pp. 13–27. Arrives at the same conclusion as that given in 8, above.

10. Bacteria as a test for the activity of the chlorophyll function in aquatic plants. See Vines, Physiology of Plants, London, 1886, p 255, Engelmann, Jour. Roy. Micr. Soc., 1881, p. 962, 1882, p. 663, 1888, p. 473, 1890, p. 80.

11. Hudson, W. H. The Naturalist in la Plata, London, 1892. Gives numerous examples of apparent re-acquirement of characters, especially habits.

12. Goodale, George L. Physiological Botany. New York, 1885. Excellent statement of the respiratory function in plants, p. 371.